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Use of Airphotos to Identify, Describe, and Manage Forest Structure of Marbled Murrelet Nesting Habitat at a Coastal British Columbia Site

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TABLE OF CONTENTS

EXECUTIVE SUMMARY 2
KEYWORDS 2
ACKNOWLEDGEMENTS 2
INTRODUCTION AND OBJECTIVES 3
STUDY AREA 3
METHODS 3
Field Sampling 3
Airphoto Interpretation 4
Sampling Design 4
Statistical Analyses 7
RESULTS 8
Land Base Polygons 8
Platform Polygons 8
Treed Polygons 8
DISCUSSION 9
Land Base Polygons 9
Importance of Stand Structure—Vertical Complexity 12
Stand Age 13
Basal Area, Crown Closure, and Height 14
MANAGEMENT CONSIDERATIONS FOR HABITAT RECRUITMENT OR RESTORATION 14
STUDY LIMITATIONS 15
CONCLUSIONS 15
REFERENCES 16
APPENDIX A: TREE SPECIES COMPOSITION OF POLYGONS, BY TYPE 18

TABLES
Table 1. Landscape Cover Classification Scheme as it applies to those polygons described for this study 5
Table 2. Attribute Classification for treed polygons within the Landscape Cover Classification Scheme 6
Table 3. Distribution of nest polygons and random polygons among landscape cover component classes 7
Table 4. Means and standard errors of attributes for nest, treed, and platform polygons 10
Table 5. Maximum likelihood estimates using Logistic Regression for nest polygons compared to platform polygons 10
Table 6. Maximum likelihood estimates using Logistic Regression for known active mid-chick nest polygons compared to platform polygons but eliminating age 10
Table 7. Maximum likelihood estimates using Logistic Regression for nest polygons compared to treed polygons 11
Table 8. Maximum likelihood estimates using Logistic Regression for known active mid-chick nest polygons compared to treed polygons 11
Table 9. Maximum likelihood estimates using Logistic Regression for nest polygons compared to treed polygons but eliminating age 11
Table 10. Maximum likelihood estimates using Logistic Regression for known active mid-chick nest polygons compared to treed polygons but eliminating age 11
Table 11. Significant Spearman's Rank Correlation coefficients between attributes for nest and treed polygons 12

FIGURES
Figure 1. Predicted conditional probability of a Marbled Murrelet using a polygon for nesting 12
Figure 2. Predicted conditional probability of a Marbled Murrelet using a polygon in which the nest will be active at mid-chick stage as age of the polygon changes 12
Figure 3. Predicted conditional probability of a Marbled Murrelet using a polygon for nesting as height of the polygon changes 13

EXECUTIVE SUMMARY

We examined stand-level habitat associations of Marbled Murrelet nest sites located by radio telemetry (1998–2000) in the Sunshine Coast area of south coastal British Columbia. We estimated amounts and types of forest structural attributes from mid-scale airphotos for 45 nest polygons (stands) using a Vegetation Resources Inventory Classification (VRI). Our first two objectives were to determine if airphoto interpretations are useful for predicting nesting habitats of Marbled Murrelets, and if so, evaluate if these interpretations can be used to assist managers select suitable candidate reserve areas for them. We found using logistic regression that of five attributes (mean height in m, mean basal area in m^2/ha, mean age in years, mean crown closure in %, and vertical complexity by class) vertical complexity best predicted which polygons murrelets will use for nesting and which polygons are likely to have a successful nest. In addition, stand age improved the conditional probability of a murrelet using a polygon for nesting, but this improvement appeared to increase at a decreasing rate for polygons >200-year old that were vertically complex. Vertical complexity is defined as >20% height differences between canopy dominants and the average tree canopy layer and as having visible canopy gaps. It is influenced by stand age, past disturbance and tree species succession. Vertical complexity has been associated with higher quality microhabitat for nests (platform branch size, and epiphyte cover) and/or as providing access into the stand for this seabird. We suggest stand age may also be a surrogate for higher quality microhabitat features associated with nest sites.

Our third objective was to determine if our findings could help prescribe restoration of managed stands and thereby re-establish potential habitat. Overall, the relationship we modelled between age and vertical complexity suggested that habitat suitable for murrelet nests may be recruited earlier if younger stands are managed for vertical complexity. We recommend further research on the value of airphoto interpretation for identifying habitats for Marbled Murrelet reserves, and for habitat restoration.

KEYWORDS

Marbled Murrelet, *Brachyramphus marmoratus*, nesting habitat associations, airphoto interpretation, forest structural attributes, vertical complexity, British Columbia

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INTRODUCTION AND OBJECTIVES

The Marbled Murrelet (*Brachyramphus marmoratus*, Family Alcidae) is a Pacific northwest seabird that nests inland[1] in forests ranging from Alaska to California. Currently, it is listed at risk in British Columbia by both the Committee on the Status of Endangered Wildlife in Canada (Rodway 1990; Hull 1999) and the provincial government (BC Ministry of Forests and BC Ministry of Environment 1999) because the total population is suspected to have declined with loss of nesting habitat, related mainly to commercial harvesting of old-growth forests.

Marbled Murrelets usually use large-diameter branches of older trees for nest platforms, although a few nests have been located on the ground in Alaska and British Columbia (Nelson 1997; Bradley and Cooke 2001), therefore nesting habitat of Marbled Murrelets is defined broadly as old-growth forest. Yet, recent research suggests that not all old-growth forest is used for nesting and that some types of old growth may be selected by Marbled Murrelets more often when they are available. In addition, Marbled Murrelets are likely to select their nesting habitat at a variety of scales (Manley 1999). At finer scales, Marbled Murrelets may select microhabitats such as the nest tree or the nest patch directly around the nest tree; at coarser scales, they may select macrohabitats such as nest stands that contain nest patches or landscapes that contain nest stands (Manley 1999).

From 1998 to 2000, the Centre of Wildlife Ecology at Simon Fraser University and the Canadian Wildlife Service led a study of Marbled Murrelet nesting habitat on the south coast of British Columbia (lat. 50°04' N, long. 124°42' W), in partnership with the Vancouver Forest Region of the British Columbia Ministry of Forests (BC Ministry of Forests). In part, the research was designed to learn more about the characteristics of Marbled Murrelet nesting habitat by using radio telemetry to locate a large sample of actual nests in locations that are both accessible and inaccessible by humans. In this Technical Report we use a portion of these nest locations to examine whether estimating amounts and types of forest structural attributes from airphotos (mid-scale, mostly ~1:15000) is a technique that can be used to describe and differentiate Marbled Murrelet nesting habitats, as has been done elsewhere for other species (Dussault et al. 2001). So far, the reliability of airphoto interpretation and the resultant forest or vegetation cover maps (Resources Inventory Committee 2001), have been assessed by using observed behaviours and habitat models or algorithms (Bahn and Newsom in press; Burger in press). But these assessments may suffer from possible biases because they do not reflect actual nests, and they may be influenced by whether or not the site is accessible by humans.

The objectives of the study were to:

- determine if airphoto interpretations—using the Vegetation Resources Inventory (VRI) classification (Resources Inventory Committee 2001)—are useful for predicting nesting habitats of Marbled Murrelets, and if so,
- evaluate if these interpretations can be used to assist managers select suitable candidate reserve areas for Marbled Murrelets, and
- help prescribe restoration of managed stands and thereby reestablish potential habitat.

STUDY AREA

The study took place on the Sunshine Coast of British Columbia, near Powell River, which is about 100 km north-northwest of the city of Vancouver. The Coastal Western Hemlock (CWH) and Mountain Hemlock (MH) biogeoclimatic zones (Meidinger and Pojar 1991) dominate the study area, and Marbled Murrelet nesting locations are found in most variants. Nests were found in the Coastal Western Hemlock dry maritime variant (CWHdm; elevation 0–600 m) which is dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) with lesser amounts of western redcedar (*Thuja plicata*). Nests were also located in the wetter variants including the Coastal Western Hemlock submontane very wet maritime (CWHvm1, elevation 0–650 m) and the Coastal Western Hemlock montane very wet maritime (CWHvm2, elevation 600–1000 m) variants. These forests are dominated by western hemlock and amabilis fir (*Abies amabilis*) with lesser amounts of western redcedar (Green and Klinka 1994). In addition, in the CWHvm2, smaller amounts of yellow cedar (*Chamaecyparis nootkatensis*) and mountain hemlock (*Tsuga mertensiana*) occur with increasing elevation and with increasing wetness of the site (Green and Klinka 1994). A number of nests were located in the cooler, higher elevation forests in the windward moist maritime variant of the MH zone (Mhmm1, elevation 1000 to ~1350 m). These forests are dominated by amabilis fir and mountain hemlock with lesser amounts of yellow cedar (Green and Klinka 1994). Extensive harvesting of old-growth has occurred in the study area, and harvesting has been concentrated at the lower elevations; less than 30% of the forested area is now old-growth (Manley 1999; Huettmann et al. submitted).

METHODS

Field Sampling

During the early summers of 1998, 1999, and 2000, at night, Marbled Murrelets were captured at sea (Whitworth et al. 1997), fitted with radio transmitters[2] using subcutaneous anchors (Newman et al. 1999), and released. The capture sites included Desolation Sound (1998–2000) and Toba Inlet (2000).

Subsequently, these individuals were located at their nest sites (usually during incubation). Most of the nesting locations were scattered within a 53-km radius of the average of the two marine capture sites, i.e., scattered between the Eldred River (east of Powell Lake) and the tributaries of Toba Inlet. Exact nesting locations were determined first by using helicopter surveys to approximate the location (within ~100-m^2 area) and then by

[1] Nests are usually within 30 km of the coastline, but may be up to 80 km inland.
[2] Advanced Telemetry Systems Model 394 was used in 1998, and Model 386 Isanti MN was used in 1999–2000.

ground telemetry using a hand-held three-dimensional Yagi antennae[1] and visual searches (Hull et al. 2001; Bradley and Cooke 2001). For inaccessible sites, locations were included as nest sites if strong, constant signals were received for at least two consecutive incubation shifts (Cam et al. submitted). Active mid-chick nests included those nests for which individuals appeared involved in the breeding process for at least 10 days after the hatching date, e.g., as determined by monitoring the feeding visits of the adult birds (Cam et al. submitted). This was a nesting success measure that could be determined for all sites. Final nest success was confirmed only if nest trees were climbed and evidence of fledging—such as down and a complete fecal ring—were found (Manley 1999; Cam et al. submitted).

Airphoto Interpretation

A large contiguous area of forest can be delineated into a number of vegetated polygons using the VRI classification (Resources Inventory Committee 2001). A polygon is, in general, equivalent to a "stand" (Daniel et al. 1979) which is the term usually used when describing the macrohabitat of Marbled Murrelets. A polygon is a portion of land of "like" or uniform cover delineated on mid-scale aerial photography for VRI (Resources Inventory Committee 2001). In BC, polygon delineation is a key phase, used in conjunction with ground sampling, to develop forest inventories. Each polygon has one value for each descriptor or attribute and there is no measure of variance of these attributes within the polygon. The polygon boundary changes with changes in mean values of the descriptors and attributes, resulting in a variety of sizes and shapes of polygons (Tables 1 and 2) that are independent of any one attribute or descriptor used in the classification.

VRI has not been undertaken for this study area, therefore we directly applied its criteria (Tables 1 and 2) to the airphotos that corresponded to the nesting locations.

The field crew plotted each nesting location onto the appropriate airphoto. Each plot was considered to be accurate within 100 m (planimetrically), with most plots likely to be accurate within 50 m. We excluded nesting locations from 1998 and 1999 if the appropriate photograph was not available or if the image had poor visual quality (i.e., from shadowing). Most airphotos were standard colour at a scale of 1:10 000 or 1:15 000, but some images were available only in black and white. Three 1:40 000 images were included because the airphoto interpreter was confident the estimates of stand structure were consistent with those at lower scales. We included one of twenty-eight nest sites from 2000 because we had airphotos for this site.

We obtained images from either Landdata BC (Timber Sale Areas), or from Weyerhaeuser BC Coastal Group and International Forest Products Limited (Tree Farm Licenses). These images dated from the mid-1990s (30 pairs), mid-1980s (11 pairs) and the mid-1970s (4 pairs). We checked if any operational activities had occurred in the vicinity of the nests since the airphotos had been taken. To avoid inconsistencies, the same highly experienced interpreter examined all the photographs.

Sampling Design

We used three levels of sampling to test for habitat selectivity of stand attributes at the polygon level and to consider habitat restoration, i.e. land base, treed, and platform.

First the photo interpreter delineated the polygon within which the nest fell as a "nest polygon", and then the interpreter delineated all polygons that were adjacent to and sharing a common boundary with the nest polygon (Tables 1 and 2). We used these adjacent polygons as our measure of habitat availability because the area of habitat available to the capture population had not yet been defined biologically (Huettmann et al. submitted). For our approach, we therefore assumed that murrelets take spatial criteria (e.g., general elevation, topography, patch size, edge, and location of food sources) into account before selecting for other attributes within the nest polygon. Our paired comparisons in the analyses helped control for differences between attributes that are due to elevational gradients, such as differences in tree height, and for other landscape-level features such as distance to sea (Hull et al. 2001).

Following delineation of the polygon boundaries, we recorded estimates of the following forest structural attributes for each polygon: tree species composition, average tree height (m), average tree basal area (m^2/ha), average crown closure (%), average vertical complexity, and average tree age (years). These attributes are reported as indicators of Marbled Murrelet habitat from studies that rely on ground searches for nests and/or through using inland detections of Marbled Murrelets (Ralph et al. 1995; Manley 1999; Bahn and Newsom in press). We did not test macrohabitat associations—such as edge, area, or shape—which spatially describe the polygon in our model because these change as the mean descriptors and structural attributes change in the forest (Tables 1 and 2). Potential limitations associated with this method are listed in the Discussion. The importance of macrohabitat associations with the location of nests within the landscape (e.g., elevation, slope, aspect) are tested and reported elsewhere (Huettmann et al. submitted).

Land base polygons. We evaluated type of nest polygons selected by Marbled Murrelets through pairing each nest polygon with a polygon randomly selected from those adjacent to and sharing a common boundary with the nest polygon. Each random polygon, hereafter called a *land base* polygon, was selected starting clockwise from the north position using a random number table. All adjacent polygons had equal probability of being selected regardless of the proportion of shared boundary and regardless of shape or size. Each nest polygon and land base polygon was described as treed or non-treed, and estimates of attributes were given (Tables 1, 2, and 3). We adjusted upwards the values of attributes (tree height, tree basal area, tree age, crown closure) for two of the land base polygons because the stand conditions were outdated by 20 years on the available airphotos.

[1] Advanced Telemetry Systems, Isanti MN.

Table 1. Landscape Cover Classification Scheme as it applies to those polygons described for this study. Minimum polygon size varies between 2 and 5 ha. For a complete description of the process used in classification see Resources Inventory Committee (2001).

Level of Classification *	Description of the polygon
Level 1, Land Base	*Vegetated*. >5% of the total surface area has trees, shrubs, herbs, and bryoids by vertical projection. *Non-Vegetated*. <5% of the total surface area has trees, shrubs, herbs, and bryoids by vertical projection.
Level 2, Land Cover Type	
Vegetated	*Treed*. ≥10% of the polygon area, by crown cover. *Non-Treed*. ≤10% of the polygon area, by crown cover.
Non-Vegetated	*Land*. >50% of polygon area covered by land. *Water*. >50% of polygon area covered by water.
Level 4, Land Cover Components	Must have a minimum contiguous piece ≥10% of the polygon area. Together land cover component percent values must equal 100%.
Vegetated	*Treed* · *Coniferous*. Total basal area of coniferous trees ≥75% of the total polygon tree basal area. · *Broadleaf*. Total basal area of broadleaf trees ≥75% of the total polygon tree basal area. · *Mixed*. Neither coniferous nor broadleaf account for≥75% of total polygon tree basal area. *Non-Treed* · *Shrub Tall*. Average height ≥2 m and polygon has >5% total vegetation cover, and >20% ground cover shrubs *or* shrubs >33% of total vegetation cover. · *Shrub Low*. Average height <2 m and polygon has >5% total vegetation cover, and ≥20% ground cover shrubs *or* shrubs >33% of total vegetation cover. · *Herbaceous* (without woody stems). Polygon has >5% total vegetation cover, ≥20% ground cover herbs *or* herbs >33% of total vegetation cover and <20% shrub cover in the polygon. · *Bryoid* (bryophytes and lichens, except crustose lichens). Polygon has >5% total vegetation cover, >50% ground cover of total vegetation cover is in bryoids and both herb and shrub cover each are <20% crown cover.
Non-vegetated	*Land* · *Bedrock* (within subclass of rock/rubble). Greatest percentage coverage by area-unfragmented, consolidated rock, contiguous with the underlying material within. · *River Sediments* (within subclass exposed land). Greatest per-centage coverage by area-silt, gravel, and sand bars associated with former river channels and present river edges.

* We do not discuss Level 3 landscape position (which is Upland) unless it is Alpine (treeless or <1% tree cover) or Wetland (water table near or above water surface).

Table 2. Attribute Classification for treed polygons within the Landscape Cover Classification Scheme, as used for this study. For a complete description of the process used in classification see Resources Inventory Committee (2001).

Attribute	Description of the polygon
Crown Closure	Percent estimate of the vertical projection of tree crowns upon the ground by each tree layer identified.
Basal Area	Total cross-sectional area (m^2/ha), at breast height, of all living trees visible to the photo interpreter in the dominant, co-dominant, and high intermediate crown positions for each tree layer in the polygon.
Species Composition	Describes live tree species present and estimates the percentage of each in the polygon by proportion of basal area or density. Species composition adds up to 100%.
Age	Average age (years) weighted by basal area of the dominant, co-dominants, and high intermediates for the leading and second species for each tree layer identified.
Height	Average height (m), weighted by basal area, of the dominant, co-dominant, and high intermediate trees for the leading and second species of each tree layer identified.
Vertical Complexity *	Subjective classification that describes uniformity of the forest canopy by estimating the total difference in height of leading species and average tree layer height, describing occurrence of canopy gaps and past or recent disturbances, and stocking patterns. · *Very Uniform*. <11% height difference, no evidence of canopy gaps or recent disturbance. · *Uniform*. 11-20% height difference, few canopy gaps may be visible, and little or no evidence of recent disturbance. · *Moderately Uniform*. 21-30% height difference, some canopy gaps may be visible, and there may be evidence of past disturbance, stocking may be somewhat patchy or irregular. · *Non-Uniform*. 31-40% height difference, canopy gaps often visible (due to past disturbance), stocking typically patchy or irregular.

* Very Uniform and Uniform were combined into one class, and Moderately Uniform and Non-Uniform into a second class, for statistical analysis.

Treed polygons. We evaluated habitat restoration of younger forests for Marbled Murrelets by projecting probabilities of polygon use as trees age or as the value of one structural attribute changed compared to another in the polygon. For these comparisons, fifteen of the land base polygons were re-selected such that they were treed (see Table 1; i.e., ≥10% of the polygon area, by crown cover), hereafter called *treed* polygons, using the same random selection method. In eliminating *non-treed* polygons, we assumed that Marbled Murrelets at the polygon scale would always choose treed over non-treed areas. This assumption was necessary because all nest polygons were classified as treed, whereas 40% of the land base polygons were non-treed (Table 3). Comparisons between a large sample of treed and non-treed polygons would emphasize their structural differences but would not help distinguish how characteristics of treed stands change over time to produce suitable murrelet habitat. Three nest polygons were completely surrounded by non-treed area, therefore we treated the treed polygon pairs for these as missing in the analyses, thus reducing our sample size.

Platform polygons. We tested for habitat selectivity of forest structure by comparing nest polygons and adjacent random polygons that had potential nest platform trees, hereafter called *platform* polygons. Potential nest platform trees were considered to be veteran trees >140 years. We defined a polygon as capable of providing nest platforms if one or more veteran tree(s) were in the polygon. We replaced, using our random selection method, seven treed polygons that did not meet the platform criterion. We treated six of the platform polygons as missing, thus reducing our sample size during further analyses, because alternative adjacent polygons with potential nest platform trees were not available.

Statistical Analyses

First, we used the Fisher Exact Test (Zar 1984) to determine whether the probability of the polygons being treed was the same for nest and land base polygons. We eliminated tree species composition (Appendix A) from the following analyses because it was diverse, did not indicate any strongly observable trends, and was likely correlated with elevation (see Study Area description) which was not tested in this study. Next, for detecting differences between structure (mean tree age in years, mean tree height in m, mean tree basal area in m^2/ha, crown closure in %) of the nest and both treed and platform polygons, we used Wilcoxon signed-rank tests on the paired replicates (Zar 1984). For the categorical variable vertical complexity, we used McNemar's Test (Agresti 1996). We combined the four classes of vertical complexity into two classes—Very-Uniform-to-Uniform, and Moderately-Uniform-to-Non-Uniform (Table 2)—because of our small sample size. We tested for associations using all the nest polygons and a subset of these polygons that were more likely to have resulted in successful fledging (see Field Sampling Methods). We defined this latter subset as the "active mid-chick subset". It includes those nest locations that were active at the mid-chick stage (see Methods) unless failure had been confirmed by climbing the tree and visually checking the nest. This subset might be biased towards habitats in inaccessible nest sites because tree climbing could not be undertaken in those cases. But, for this exploratory approach, we attempted to reduce variance introduced when including sites with known nest failures. Therefore, we tested for this potential bias between ground-accessed and inaccessible nest polygons (and active mid-chick polygons) using ranked one-way analysis of variance for the continuous variables, and a chi-square test for vertical complexity (Zar 1984).

Table 3. Distribution of nest polygons and random polygons among landscape cover component classes.

	Polygon type			
	Nest	**Land Base**	**Treed**	**Platform[a]**
Treed 100%				
Coniferous	39	23	34	35
Broadleaf	1	2	4	1
Mixed	1			
	n=41	n=25	n=38	n=36
Treed <100%				
Bare Rock	3			
Bryoid			2	1
Shrub Low	1			
Shrub Tall		1	1	2
Herbaceous		1	1	0
	n=4	n=2	n=4	n=3
Non-Treed [b]				
Shrub Low		3	1	1
Shrub Tall		3	1	1
Bryoid		6	1	1
Bare Rock		4		
Herbaceous		1		
River Sediments		1		
	n=0	n=18	n=3	n=3

[a] Excluded those polygons without suitable nest platforms (n=7).

[b] Excluded these polygons (n=3) and paired nest polygon.

We determined whether polygon attributes are useful predictors of the Marbled Murrelet's nesting habitats and demonstrated relationships between the attributes using a logistic stepwise regression model to determine a 'resource selection function' (Brennan et al. 1984; Manly et al. 1993). This function identifies those habitat attributes that best convey the probability of a Marbled Murrelet nest occurring within a polygon. The resource selection function is directly proportional to the unknown 'resource selection *probability* function'. It can be estimated by modelling the conditional probability that an observation having a particular set of habitat attributes will be found at a nest polygon rather than a treed (or platform) polygon, given that the observation is in one of the two polygons (p.101 in McCullagh and Nelder 1989; p.126 in Manly et al. 1993). The logistic regression is of the form:

$$\log\left(\frac{\tau_k}{1-\tau_k}\right) = \beta_0 + \beta_1 x_{1k} + \beta_2 x_{2k} + \cdots + \beta_p x_{pk} \quad (1)$$

where

τ_k is the probability that an observation having a particular set of habitat attributes $\{x_1, x_2, \ldots, x_p\}$ will be found in the nest polygon rather than the treed (or platform) polygon, given that it is one of these locations;

$\beta_0, \beta_1, \beta_2, \ldots, \beta_p$ are the regression attributes,

and the observations are indexed by $k = 1,2,\ldots,42(or\,39)$

(or for active mid-chick nest polygons $k = 1,2,\ldots,19(or\,18)$).

Using the stepwise procedure, those attributes that best predicted the observed were retained, thus producing a simplified model with $q \leq p$ regression attributes (SAS 2000). In other words, the model becomes:

$$\log\left(\frac{\tau_i}{1-\tau_i}\right) = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \cdots + \beta_q x_{qi} \quad (2)$$

We will discuss Equation 2 in the remainder of the report, even though the resource selection function is usually of the form

$$w_i = \exp\left(\beta_1 x_{1i} + \beta_2 x_{2i} + \cdots + \beta_q x_{qi}\right).$$

Initially we included all five attributes as covariates in our comparisons with treed (or platform) polygons to determine which attribute(s) best-predicted use of sites for nesting. Then, for the comparisons using treed (and platform) polygons, we reran the models but eliminated "age" as a covariate. This enabled us to explore differences in stand structure separately from differences in age, where age represents time, but forest structure does not always reflect age (Pipp et al. 2001). We used Spearman's Rank Correlation coefficients to examine if statistically significant relationships had occurred between the attributes (Zar 1984).

RESULTS

We quantified structural attributes of polygons for twenty of the twenty-three 1998 nesting locations. Three of the twenty locations were within the same polygon and were therefore used as a single sample to avoid weighting by this general area. For 1999, we used twenty-six of the thirty-three nesting locations. This gave us a total of forty-five nest polygons from forty-seven nesting locations including the one nest polygon for 2000. The active mid-chick subset included 49% (22/45) of the locations, but this number should not be interpreted for nesting or fledgling success. We could access only 44% (20/45) of the nest sites and 32% (7/22) of the active mid-chick subset by ground. We found no significant differences (P>0.10) between accessible and inaccessible nest polygons or active mid-chick polygons for the attributes tree age, tree height, and vertical complexity. But for basal area, accessible nest polygons differed marginally from inaccessible nest polygons (P=0.051; accessible average 66.5 m^2/ha, SE 5.7; inaccessible average 47.1 m^2/ha, SE 9.4) although not for the active mid-chick subset (P=0.81; accessible average 57.9 m^2/ha, SE 8.9; inaccessible average 54.0 m^2/ha, SE 6.6). Crown closure between accessible and inaccessible nest polygons did not differ significantly (P=0.92; accessible average 49.7%, SE 3.9; inaccessible average 47.8%, SE 9.6), although it did differ significantly between polygons in the active mid-chick subset (P=0.041; accessible average 36.4%, SE 5.9; inaccessible average 50.3%, SE 4.6).

Land Base Polygons

Forty-four percent (20/45) of the land base polygons were not fully treed, with 40% (18/45) lacking any treed cover, whereas all nest polygons were treed with only 9% (4/45) not fully treed (Tables 1 and 3). Non-treed land base polygons, by definition having <10% crown cover, were characterized by shrub, bryoid, herb, and bare rock cover. The difference between the proportion of treed land base polygons and treed nest polygons was significant (n=90, Fisher exact P=9.06 x 10^{-7}). An additional 18% (8/45) of the land base polygons were post-fire or post-harvest regeneration (<140 years old if coniferous) or deciduous polygons.

Platform Polygons

We used 7/45 (16%) platform polygons for which the mean attribute estimates of the polygons reflected the younger trees (5 coniferous <140 years and 2 broadleaf) that dominated the polygon, instead of the potential platform trees within the polygon. We retained these polygons for comparison because two of the coniferous nest polygons were 80 years old and one broadleaf nest polygon was 40 years old using the Vegetation Resources Inventory criteria. In addition, three nests are now confirmed in veteran trees in mature stands (Manley et al. 1999; Cooke unpublished data for 1999 and 2001[1]). One nest was also confirmed in an old red alder tree in a mixed conifer/broadleaf area in 2000 (Bradley and Cooke 2001).

We found nest and active mid-chick polygons were more vertically complex and significantly older than platform polygons (Table 4). But vertical complexity was only marginally significant for the active mid-chick subset (P=0.06), and we suspect age differences were influenced by our use of the seven platform polygons <140 years. The logistic stepwise regression confirmed that vertical complexity, but not age, partially explains differences between nest polygons and the active mid-chick subset and platform polygons (Tables 5 and 6). The conditional probabilities for a Marbled Murrelet nesting in a Moderately-Uniform-to-Non-Uniform polygon (P=0.64; 0.75 and 0.50 upper and lower 95% confidence intervals respectively), or having an active mid-chick nest in these polygons (P=0.68; 0.83 and 0.48 upper and lower 95% confidence intervals respectively), were similar. For Very-Uniform-to-Uniform polygons, the conditional probabilities of use were also similar for nest polygons (P=0.34; 0.53 and 0.20 upper and lower 95% confidence intervals respectively) and active mid-chick polygons (P=0.33; 0.59 and 0.15 upper and lower 95% confidence intervals respectively).

Treed Polygons

We found significant differences (P<0.05) between nest polygons (and the active mid-chick subset) and treed polygons for age, height, basal area, and vertical complexity (Table 4). Crown closure did not significantly differ between the nest and treed polygons, although it did between active mid-chick and treed polygons (P=0.04), but with small differences between the means. The active mid-chick nest polygons had lower percents of crown closure.

The stepwise logistic regressions using all nest and active mid-

[1] Fred Cooke, Centre of Wildlife Ecology, Simon Fraser University, Burnaby, BC, unpublished data, 1999 and 2001.

chick polygons compared to treed polygons both produced models retaining age and vertical complexity as significant predictors (Tables 7 and 8). The non-significant Hosmer and Lemeshow Goodness of Fit statistics suggest these models have good fit (Tables 7 and 8). The attribute vertical complexity, regardless of polygon age, improved the conditional probabilities that a Marbled Murrelet would use a polygon and have a nest successful to at least the mid-chick stage. This is demonstrated through contrasting the conditional probability curves for the Very-Uniform-to-Uniform polygons to the curves for the Moderately-Uniform-and-Non-Uniform polygons (Figures 1 and 2). Vertical complexity in combination with age appears to have more strongly predicted those polygons likely to have active mid-chick nests, than those likely to be used for nesting.

Curves for Very-Uniform-to-Uniform and Moderately-Uniform-to-Non-Uniform polygons suggest that polygon suitability does improve as the mean polygon age extends beyond 140 years, which is considered the minimum age for providing murrelet habitat (BC Ministry of Forests and BC Ministry of Environment 1999). In Moderately-Uniform-to-Non-Uniform polygons that are approximately 200–300 years old, suitability increases at a decreasing rate; whereas, in Very-Uniform-to-Uniform polygons, suitability increases at an increasing rate (Figures 1 and 2). Younger polygons, whether of uniform or complex structure, are not likely to be used for nesting.

Vertical complexity was the only highly significant variable to enter the model for all nest polygons when we eliminated age as a covariate; but height also entered the model as a marginally significant predictor (P=0.06) (Table 9, Figure 3). Height is significantly (P<0.05) correlated with age and basal area (Table 11). Age is significantly (P<0.05) correlated with basal area and crown closure as well as height (Table 11). The final model, using active mid-chick polygons, did not retain height (Table 10) but simply supports the view that nest polygons active at the mid-chick stage are more likely to occur in Moderately-Uniform-to-Non-Uniform polygons (P=0.85; 0.95 and 0.62 upper and lower 95% confidence intervals respectively) than in Uniform polygons (P=0.24; 0.46 and 0.10 upper and lower 95% confidence intervals respectively).

DISCUSSION

Land Base Polygons

Initially, given our method for selecting adjacent polygons, we had assumed that most land base polygons would be treed if Marbled Murrelets select nest sites in larger areas of continuous forest (Manley 1999; Burger et al. 2000; Raphael et al. in press). Even if older forests were limited to higher elevations as in some parts of the study area, we had assumed that Marbled Murrelets would select larger tracts relative to those available and that nest polygons would mostly be surrounded by treed polygons. Alternatively, if the older forest was no longer continuous as a result of forestry operations or fire disturbance, we expected that most land base polygons would still be classified as treed but in younger seral stages. Instead, the significantly higher proportion of non-treed land base polygons that we selected adjacent to the treed nest polygons suggests that murrelets may not necessarily avoid nesting in areas of forest adjacent to openings >2 ha (minimum polygon size for VRI). This finding appears consistent with the finding for positive selectivity and success at edges by Huettmann et al. (submitted), which incorporates the same sample of nests. But we did not measure distances between nest locations and edge of the non-treed polygon to test for edge effects, nor did we make landscape-level comparisons. Hamer and Nelson (1995), Manley (1999), and Raphael et al. (in press) report that nest locations may be associated with natural or human-created gaps. Although many of the land base polygons, which are a minimum size of 2 ha, are likely larger than these gaps, larger openings could function in a similar manner for Marbled Murrelets if they are important for stand access. Therefore we hypothesize that either:

- Nesting locations are spatially selected adjacent to open areas, such as non-treed polygons, because these openings enhance flight access into the forest stand (Nelson 1997). Flight access is important because the Marbled Murrelet's wing design makes take off and landing difficult (Pennycuick 1987). Exiting the forest is also a potential risk because once grounded (as a number of chicks have been found), Marbled Murrelets may have difficulty flying away from the forest floor given their webbed feet and long, narrow wings (Nelson 1997). The additional land base polygons (18%) that were treed with younger forest (<140 years) and the significant height difference that was found between treed polygons and nest polygons also support this hypothesis. Nest sites adjacent to areas with shorter trees could function similarly to those that are non-treed by providing better access at the forest edge.

- A large portion of available suitable habitat occurs in smaller discontinuous forested areas because of the mountainous topography and/or forest harvesting history of this area (Manley 1999; Huettmann et al. submitted). Therefore, the higher-than-expected proportion of non-treed land base polygons may be an artefact of the sampling design because of use of the adjacency rule (see Study Limitations).

All nest polygons in our sample using VRI were classified as treed, and this indirectly supports our assumption for the analyses that Marbled Murrelets select treed polygons before non-treed polygons. If non-treed areas that meet microhabitat and macrohabitat requirements of Marbled Murrelets are relatively rare, this could explain why most nest polygons were treed (Hamer and Nelson 1995). At least one cliff nest site was confirmed in the study area in 2000 (Bradley and Cooke 2001) and other potential cliff nest sites are reported for this and other areas (Nelson 1997; Cooke unpublished[5]). Our assumption does not preclude that cliff nests could occur in treed polygons, or that non-treed polygons may be used if limited treed habitat is available. Neither do we suggest that Marbled Murrelets will avoid

[5] See Footnote 4.

Table 4. Means and standard errors of attributes for 45 nest (and 22 mid-chick) polygons, 42 (and 19) treed polygons, and 39 (and 18) platform polygons. Results from Wilcoxon Paired Sample signed-rank tests or McNemar's tests are separately reported between nest (and mid-chick) polygons (sample sizes adjusted for paired tests) and treed and platform polygons.

Attribute	Polygon type	Mean (standard error)	Paired test (nest)	P	Mean (standard error)	Paired test (mid-chick)	P
Crown Closure	Nest [b]	48.2 (2.7)			47.0 (3.4)		
	Platform	49.7 (2.6)	-41.5	0.460	50.0 (4.4)	-26.5	0.220
	Treed	51.5 (2.7)	-90.0	0.170	52.4 (4.1)	-47.5	0.040
Age	Nest [b]	255.3 (11.2)			281.8 (11.2)		
	Platform	215.1 (16.1)	55.5	0.010	213.9 (24.8)	21.5	0.030
	Treed	166.4 (17.9)	150.5	<0.001	143.7 (26.8)	56.5	<0.001
Height	Nest [b]	29.8 (1.4)			29.9 (1.8)		
	Platform	26.4 (1.7)	95.0	0.150	25.4 (2.8)	23.0	0.340
	Treed	20.8 (1.8)	255.5	<0.001	17.6 (2.6)	68.0	<0.001
Basal Area	Nest [b]	55.7 (4.4)			55.2 (5.2)		
	Platform	48.5 (4.3)	68.5	0.330	47.9 (6.9)	16.5	0.490
	Treed	38.8 (4.3)	198.0	0.010	33.5 (6.6)	57.0	0.020
Vertical Complexity [a]	Nest [b]	1 n=9 2 n=33			1 n=4 2 n=15		
	Platform	1 n=19 2 n=20	5.6 [c]	0.020	1 n=10 2 n=8	3.6 [c]	0.060
	Treed	1 n=27 2 n=15	13.5 [c]	<0.001	1 n=16 2 n=3	10.3 [c]	<0.001

[a] Category 1 is Very-Uniform-to-Uniform, Category 2 is Moderately-Uniform-to-Non-Uniform.
[b] Or mid-chick polygons. [c] McNemar's test.

Table 5. Maximum likelihood estimates using Logistic Regression for nest polygons compared to platform polygons but eliminating age as a covariate n=39. Reduction of Deviance ($-2[\text{LogL}(\mu) - \text{LogL}(\mu, \beta_1)] = 6.55$, 1 df, $P<0.01$). The Hosmer and Lemeshow test is not applicable because there are there are no continuous predictors in the model.

Parameter	Degrees of freedom	Estimate	Standard error	Chi-square	P
Intercept	1	0.5596	0.2803	3.9855	0.0459
Vertical Complexity (Very-Uniform-to-Uniform polygons)	1	-1.2014	0.4808	6.2429	0.0125

Table 6. Maximum likelihood estimates using Logistic Regression for known active mid-chick nest polygons compared to platform polygons but eliminating age as a covariate n=18. Reduction of Deviance ($-2[\text{LogL}(\mu) - \text{LogL}(\mu, \beta_1)] = 4.61$, 1 df, $P<0.03$). The Hosmer and Lemeshow test is not applicable because there are no continuous predictors in the model.

Parameter	Degrees of freedom	Estimate	Standard error	Chi-square	P
Intercept	1	0.7536	0.4287	3.0899	0.0788
Vertical Complexity (Very-Uniform-to-Uniform polygons)	1	-1.4467	0.6956	4.3261	0.0375

Table 7. Maximum likelihood estimates using Logistic Regression for nest polygons n=42 compared to treed polygons (Figure 1). Reduction of Deviance ($-2[\text{LogL}(\mu) - \text{LogL}(\mu, \beta_1, \beta_2)] = 21.52$, 2 df, $P<0.0001$) and Hosmer and Lemeshow Test (Chi-Square 6.05, 5 df, P=0.30).

Parameter	Degrees of freedom	Estimate	Standard error	Chi-square	P
Intercept	1	-0.7684	0.7783	0.9746	0.3235
Age	1	0.00627	0.00280	5.0236	0.0250
Vertical Complexity (Very-Uniform-to-Uniform polygons)	1	-1.2471	0.5424	5.2864	0.0215

Table 8. Maximum likelihood estimates using Logistic Regression for known active mid-chick nest polygons compared to treed polygons n=19 (Figure 2). Reduction of Deviance ($-2[\text{LogL}(\mu) - \text{LogL}(\mu, \beta_1, \beta_2)] = 24.37$, 2 df, $P<0.0001$) and Hosmer and Lemeshow Test (Chi-Square 1.14, 5 df, P=0.95).

Parameter	Degrees of freedom	Estimate	Standard error	Chi-square	P
Intercept	1	-1.9090	1.67020	1.3064	0.2531
Age	1	0.0137	0.00603	5.1262	0.0236
Vertical Complexity (Very-Uniform-to-Uniform polygons)	1	-2.0649	0.89060	5.3759	0.0204

Table 9. Maximum likelihood estimates using Logistic Regression for nest polygons compared to treed polygons but eliminating age as a covariate n=42 (Figure 3). Reduction of Deviance ($-2[\text{LogL}(\mu) - \text{LogL}(\mu, \beta_1)] = 19.77$, 2 df, $P<0.0001$) and Hosmer and Lemeshow Test (Chi- Square 5.57, 7 df, P=0.59).

Parameter	Degrees of freedom	Estimate	Standard error	Chi-square	P
Intercept	1	-0.6180	0.8453	0.5345	0.4647
Height	1	0.0484	0.0265	3.3433	0.0675
Vertical Complexity (Very-Uniform-to-Uniform polygons)	1	-1.3390	0.5420	6.1034	0.0135

Table 10. Maximum likelihood estimates using Logistic Regression for known active mid-chick nest polygons compared to treed polygons but eliminating age as a covariate n=19. Reduction of Deviance ($-2[\text{LogL}(\mu) - \text{LogL}(\mu, \beta_1)] = 16.66$, 1 df, $P<0.0001$). The Hosmer and Lemeshow test is not applicable because there are no continuous predictors in the model.

Parameter	Degrees of freedom	Estimate	Standard error	Chi-square	P
Intercept	1	1.7346	0.6262	7.6725	0.0056
Vertical Complexity (Very-Uniform-to-Uniform polygons)	1	-2.8978	0.8091	12.8265	0.0003

non-treed areas with sufficient microhabitat and macrohabitat attributes for nesting, such as mossy nest platforms with cover (Bradley and Cooke 2001; Marks and Kuletz 2001).

Importance of Stand Structure—Vertical Complexity

Vertical complexity was an important attribute for predicting Marbled Murrelet use of a polygon and for predicting whether the nest would remain active in the polygon at least until the mid-chick stage. Polygons selected for nesting had >20% height differences between canopy dominants, and the average tree canopy layer and had visible canopy gaps. Vertical complexity may be influenced by stand age, species (succession as relates to tree shade tolerance), and degree and age of past disturbance (Resources Inventory Committee 2001). Vertical complexity may be an important habitat attribute because multi-

Table 11. Significant (P<0.05) Spearman's Rank Correlation coefficients (r) between attributes for nest and treed polygons.

Attributes	Crown Closure	Age	Height
Crown Closure	1		
Age	-0.26	1	
Height	ns	0.65	1
Basal Area	0.38	0.49	0.78

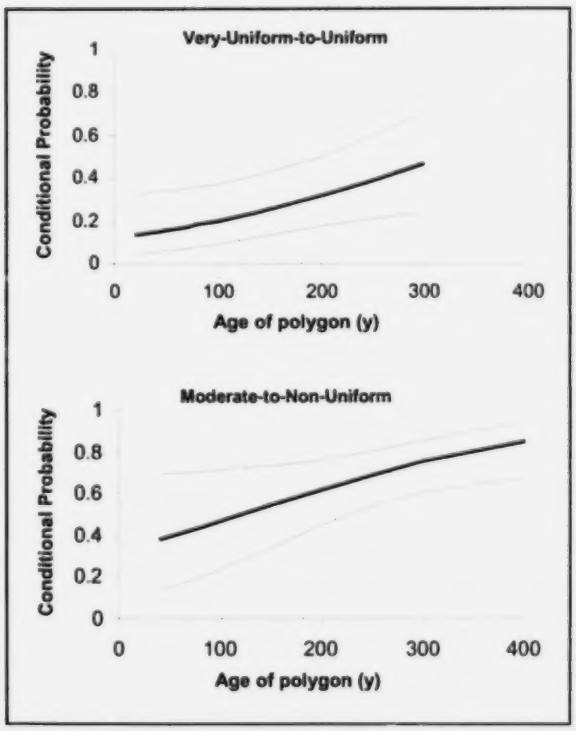

Figure 1. Predicted conditional probability of a Marbled Murrelet using a polygon for nesting, including upper and lower 95% confidence intervals, as age of the polygon changes within two classifications of vertical complexity:

$\tau_k = \exp(-0.768 + 0.006\ Age_k - 1.247\ vertical\ complexity_k) \div [1 + \exp(-0.768 + 0.006\ Age_k - 1.247\ vertical\ complexity_k)]$.

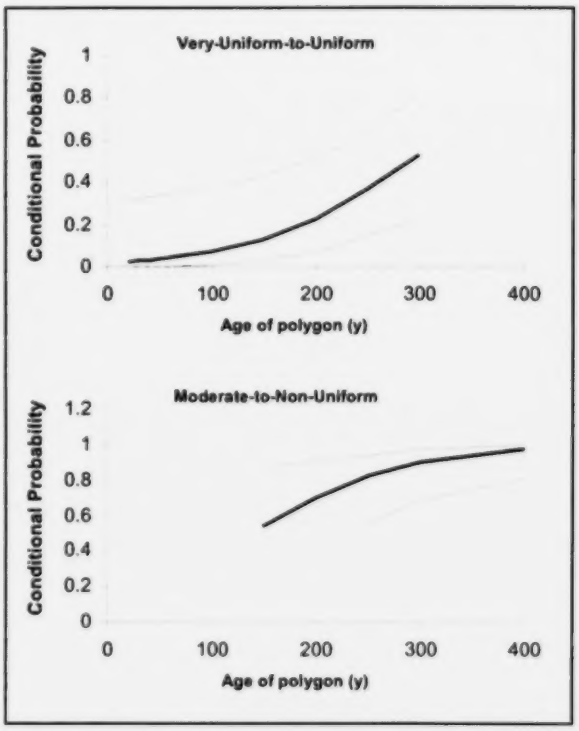

Figure 2. Predicted conditional probability of a Marbled Murrelet using a polygon in which the nest will be active at mid-chick stage as age of the polygon changes, including upper and lower 95% confidence intervals, within two classifications of vertical complexity:

$\tau_k = \exp(-1.909 + 0.014\ Age_k - 2.065\ vertical\ complexity_k) \div [1 + \exp(-1.909 + 0.014\ Age_k - 2.065\ vertical\ complexity_k)]$.

layer canopies have been associated with breeding habitat quality (e.g., cover) while providing openings in the canopy to access the nest (Hamer and Nelson 1995; Grenier and Nelson 1995; Manley 1999; Burger in press). Furthermore, depending on overall forest structure, Manley (1999) suggests that canopy openings (gaps) may be important for murrelets to access some sites (e.g., shorter forests), whereas gaps between different strata (co-dominant and dominant) may be more important for other sites (e.g., taller forests). The attribute of vertical complexity used by VRI encompasses both these elements of forest structure (vertical stratification and horizontal gappiness). Vertical complexity may also explain how murrelets exploit habitats over which other structural attributes—such as height—vary. For example, suitability of polygons with shorter trees improves if the overall polygon is more vertically complex.

Our finding that vertically complexity improves the probability of a murrelet nesting in a polygon is supported by a number of studies which use varying approaches. Studies that use the standard deviation of stand height as a measure of vertical complexity have shown that higher occupancy stands are more vertically heterogeneous than unused or low occupancy stands (Bahn 1998; Burger et al. 2000). Bahn and Newsom (in press) used the VRI attribute of vertical complexity as a variable in their habitat suitability model for the Clayoquot Sound Area, Vancouver Island. Values were taken from VRI maps delineated from airphotos (Resources Inventory Committee 2001). Their preliminary individual suitability index (SI), which ranges between 0 and 1, was 1 for vertical complexity for both Moderate and Non-Uniform classes; whereas for Very Uniform and Uniform classes the SI was 0.09 and 0.66 respectively. They also reported that significant relationships existed between vertical complexity and structures relevant to murrelets that they measured in habitat plots. These variables included epiphyte cover and epiphyte thickness, but a non-significant relationship was determined between vertical complexity and platform density.

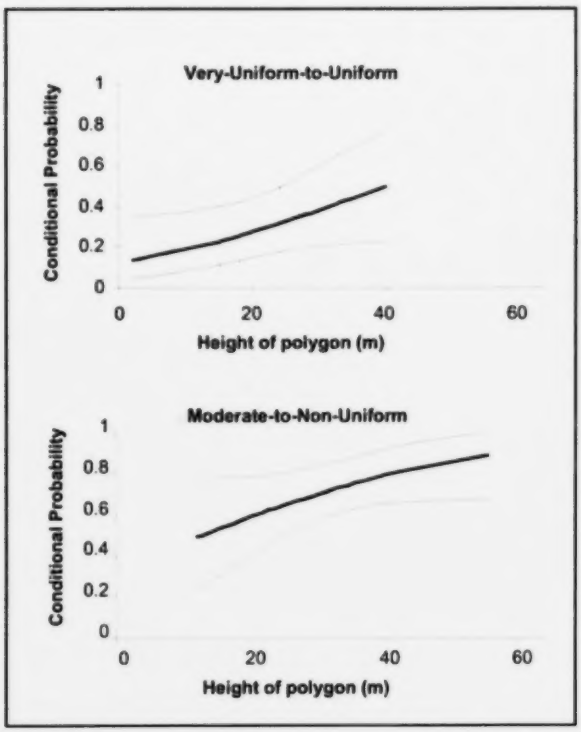

Figure 3. Predicted conditional probability of a Marbled Murrelet using a polygon for nesting as height (m) of the polygon changes, including upper and lower 95% confidence intervals, within two classifications of vertical complexity:

$\tau_x = \exp(-0.618 + 0.048 \cdot height_x - 1.339 \cdot vertical\ complexity_x) + [1 + \exp(-0.618 + 0.048 \cdot height_x - 1.339 \cdot vertical\ complexity_x)]$.

Lindsay and Leigh-Spencer (1999) used airphotos for habitat planning for Marbled Murrelets on TFL 46 on southwestern Vancouver Island, British Columbia. They assessed stands for presence and abundance of suitable nest trees defined by tree size, tree crowns with larger branches, tree species, and canopy closure (or flight access). These attributes imply a measure of vertical complexity. They eliminated stands with dense, homogeneous crowns; then, using ground transects, they estimated abundance of platforms (>15 cm diameter branches) and assessed platform quality (epiphyte thickness and cover) for the remaining stands. Their results indicated that stands identified as suitable on airphotos did not always correlate with those features suitable for nest platforms (i.e., trees with large branches or mossy platforms). They recommended that airphotos be used to identify candidate areas, but that ground transects or overhead helicopter flights are better for evaluating canopy structure and platform potential for final selection. Therefore, this study and Bahn and Newsom (in press) both suggest that vertical complexity may be associated with Marbled Murrelet habitat because of availability of suitable nesting microhabitat, as well as nest access.

But not all polygons used by Marbled Murrelets were vertically complex; for example, 22% of the nest polygons were classified as Uniform. This may partially reflect limitations of VRI because polygon estimates are based on the average, thus smaller vertically complex patches of platform trees could occur within the polygon but not be recognized in the overall estimate. In addition, vertical complexity may be less important if murrelets consider other factors more important, or when alternative habitats can function similarly to those that are more vertically complex.

Stand Age

Our comparison using treed polygons confirms earlier reported findings that forest stands used by Marbled Murrelets are not only more likely to be structurally complex, but they are likely to be older (Ralph et al. 1995). The logistic regression models

support the notion that, as the forest ages, the conditional probability of use for nesting and having a successful nest at the mid-chick stage, improves. Forests more than 140 years old are often considered as potential nesting habitat for Marbled Murrelets (BC Ministry of Forests and BC Ministry of Environment 1999), but habitat quality of polygons was predicted to potentially improve with polygon age beyond this minimum. Age alone can be a strong predictor of nest polygon selection, yet if age is used exclusively to predict habitat use, managers will inadvertently select some less suitable habitats. In addition, use of the average age of a polygon may potentially mask availability of suitable nesting habitat if it occurs patchily within the polygon. For example, two coniferous nest polygons were estimated as 80 years old, although nest trees within were likely older[6]. The youngest coniferous polygon with an active mid-chick nest was 150 years (Moderately-Uniform-to-Non-Uniform polygon).

Although forest structure is not always consistent with age (Grenier and Nelson 1995), for the samples in this study, age—rather than the attributes mean tree height, mean tree basal area, or crown closure—appears to better describe the variation between types of polygons. Age itself is not a direct measure of structure but rather a measure of time that can in turn reflect and summarize variation in structure (Pipp et al. 2001). Our results suggest that age is probably a surrogate for microhabitat features such as platform size and number and amount of epiphyte cover. Bahn and Newsom (in press) found that the VRI estimates of mean tree age for mapped polygons of Clayoquot Sound were significantly correlated with density of platforms/ha, numbers of trees with platforms/ha, epiphyte cover, epiphyte thickness, and tree height and deviation.

Basal Area, Crown Closure, and Height

Mean basal area differed significantly between nest and treed polygons, but not between nest and platform polygons. Mean tree basal area was not selected, in addition to vertical complexity and age or vertical complexity and height, as a significant predictor of nest or active mid-chick polygons. Basal area may be a poorer variable for describing murrelet habitat in a managed landscape such as the study area because denser, younger stands—or older, higher elevation stands with smaller diameter trees—can have equivalent basal area compared to sparser older stands with larger diameter trees. Greater mean basal area was marginally associated with accessible nest polygons, although not with accessible active mid-chick polygons, which could potentially reflect relationships between site productivity, topography, and accessibility. But our models using all nest polygons are likely unbiased by this because they include both accessible and inaccessible nest polygons.

Crown closure was also not selected for any of the models as a significant predictor of murrelet habitat. The comparison between accessible and inaccessible mid-chick polygons suggests that crown closure was significantly lower for accessible polygons, indicating a bias may have been introduced by eliminating failed climbed trees from accessible sites. Thus, the difference between crown closure of treed polygons and active mid-chick polygons may actually have been greater than indicated by our measures. But, if so, our result of lower crown closures of active mid-chick polygons contradicts the generally reported relationship that stands with more murrelet activity have greater canopy closures (Hamer 1995; Ralph et al. 1995; Manley 1999), although crown closure at the nest patch within the stand may be lower (Manley 1999). However, sites with very low crown closures are suggested as potentially unsuitable if they fail to provide cover over suitable nest trees, while sites with very high crown closures may be unsuitable if they limit murrelet access into the stand (Bahn and Newsom in press). Our model may not have been suitable for detecting this type of relationship. We suspect that the difference in crown closure between treed and active mid-chick polygons could have resulted from our inclusion of younger uniform stands in the treed polygon sample because these denser polygons often have higher crown closures.

Height improved predictions of nest polygon use when age was excluded from the model using treed polygons. This suggests a relationship between complexity and height, where vertical complexity may improve conditional probability that polygons dominated by shorter trees will be used for nesting. Bahn and Newsom (in press) found both tree height and deviation to have significant relationships with vertical complexity and other structures relevant to murrelets (such as epiphyte cover and thickness). They retained the VRI attributes of height, basal area, and crown closure as useful predictors in their model for Clayoquot Sound. That this result is contrary to ours may reflect the overall differences between Clayoquot Sound and this study area, different sampling approaches taken (combining ground vegetation/audiovisual detection/nest information compared to radio telemetry), differing biases in the two sampling approaches, or model development and scale.

MANAGEMENT CONSIDERATIONS FOR HABITAT RECRUITMENT OR RESTORATION

The conditional probability curves demonstrate that young, uniform, polygons have a lower probability of nest use by murrelets than those polygons of the same age that are more vertically complex. The model in this study supports the notion that managing for vertical complexity could improve the condition of a stand for Marbled Murrelet habitat at an earlier stage, than if the stand is uniformly managed. Silvicultural manipulations could include using longer rotations than those typically used on the Coast (60–80 years) or using alternative harvesting methods (Franklin et al. 1997).

The low conditional probability of use of both uniform or complex stands <150 years old, and the increased probability of use as stands age beyond 150 years, emphasizes that a minimum age threshold may occur before forests can achieve adequate microhabitat for murrelet nests. Microhabitat features include epiphyte cover and branch diameters (Burger in press).

[6] See Footnote 4.

Their availability over time is important for conservation planning (Ralph et al. 1995); for example, many epiphytic bryophyte species can take 100–400 years to develop (Marcot 1997) and may do less well in younger stands because of changes in light penetration and wetting and drying cycles (Lesca et al. 1991). In addition, epiphytes often lack the ability to widely disperse, thus retention of veteran trees across rotations can be important not only to ensure some potential nesting platforms in the next rotation, but because veteran trees can also provide source populations of epiphytes (Franklin et al. 1997; Marcot 1997).

Alternative silviculture treatments, such as thinning, can also be used to manipulate vertical stratification and horizontal gappiness—both are components of vertical complexity—as well as to accelerate stem and branch growth (Hayes et al. 1997; Ralph et al. 1995; Debell et al. 1997). Large branches may better develop in widely spaced stands with trees adjacent to gaps or openings (Hayes et al. 1997). Timing of thinning may be critical to accelerate development of old-growth-type structures such as large branches (Barbour et al. 1997).

STUDY LIMITATIONS

• We assumed for these analyses that if a polygon has a desirable structure it will be selected whether large or small (in this case, a 2-ha minimum) compared to an adjacent polygon. But in making this assumption, the model does not address whether there is a minimum size at which a Marbled Murrelet will not use a polygon even if it has suitable structure. Huettmann et al. (submitted) found no evidence for such a restriction in the same study area. The model also may fail to detect differences if Marbled Murrelets select for larger areas of forest characterized by a certain combination of attributes because of more nesting opportunities. In other words, the study does not address whether the chance of a randomly behaving bird selecting the nest polygon versus the adjacent polygon is influenced by polygon size (e.g., proportional or other).

This is a limitation of our method, which used airphotos that were not orthorectified. But it is also a limitation of VRI where adjacent polygons may have some attributes in common (e.g., vertical complexity) but others differ (e.g., species composition). For example, birds may not perceive that the two polygons are different if vertical complexity is the same for both and this is the criterion that they are selecting.

• Another limitation of our method is that for some of the platform polygons with suitable nest trees and for several nest polygons, the polygon estimates reflect the average of the polygon and not necessarily that of the platform or nest trees. In addition we include four nest polygons that were defined as treed but had <100% cover. Therefore, we used a number of assumptions when making comparisons at the polygon scale that ignore availability of habitat in patches within polygons.

• Now that the area of available habitat has been defined (Huettmann et al. submitted) for the study birds, we recommend as a next stage to this research the use of orthorectified airphotos of all nest sites (1998-2001) for comparing nest polygons to polygons selected randomly in the landscape. This comparison would allow researchers to:

1) address any potential bias regarding the sampling design and polygon size,

2) test whether polygons defined by VRI or alternative criteria are more useful for describing Marbled Murrelet habitat,

3) include non-treed nest polygons if they are delineated from the 1999–2001 samples,

4) include those nest polygons that could not be paired with treed or platform polygons, and

5) develop a broader model including both spatial parameters and stand structural characteristics.

• At this stage the VRI interpretation using the ground measurements from those nest locations that were accessible has not been confirmed. Photo imagery interpretation at the scale applied is usually accurate ±10–15% (Resources Inventory Committee 2001), although higher inaccuracies are reported at finer scales (Bahn and Newsom in press).

• The attribute crown closure may not be suitable for the logistic regression model if habitat suitability of stands with low or high crown closures is low for Marbled Murrelets, whereas optimum suitability is somewhere in between.[7]

• The study area reflects a particular topography and harvesting history, which should be taken into consideration if these results are applied to other areas.

CONCLUSIONS

• Vegetation Resources Inventory maps (Resources Inventory Committee 2001) will likely be useful for developing habitat algorithms or models at the polygon level. But, more research is required to examine habitat associations of Marbled Murrelets at the polygon level and to test the use of airphotos as a management tool.

• The Vegetation Resources Inventory attributes—vertical complexity and tree age (and possibly tree height)—may best help identify those stands, relative to the adjacent area, that are likely more suitable for management as murrelet reserves. These attributes could be directly evaluated on airphotos if the area of interest is unmapped. But consideration should be given to using the complete classification exercise for polygon delineation.

• Managing younger stands to enhance vertical complexity may potentially restore habitat quality for murrelets at an earlier age than those uniformly managed.

[7] V. Bahn, Department of Wildlife Ecology, University of Maine, ME; personal communication, December 2001.

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APPENDIX A: TREE SPECIES COMPOSITION OF POLYGONS, BY TYPE

Species composition [a]	Polygon type		
	Nest n=45	Treed n=42	Platform n=39
Amabilis fir	1	1	1
Amabilis fir/mountain hemlock	0	1	1
Amabilis fir/mountain hemlock/yellow cedar	2	2	2
Western redcedar/Douglas-fir	1	1	1
Western redcedar/amabilis fir	1	0	0
Western redcedar/amabilis fir/mountain hemlock	1	1	1
Western hemlock/Douglas-fir	1	0	0
Western hemlock/Douglas-fir/broadleaf	0	1	0
Western hemlock/amabilis fir	8	7	5
Western hemlock/amabilis fir/Sitka spruce [b]	1	0	0
Western hemlock/amabilis fir/yellow cedar	0	2	2
Western hemlock/amabilis fir/broadleaf	0	1	0
Western hemlock/western redcedar	6	9	8
Western hemlock/western redcedar/Douglas-fir	3	1	1
Western hemlock/western redcedar/amabilis fir	17	10	12
Western hemlock/western redcedar/amabilis fir/yellow cedar	1	1	1
Western hemlock/western redcedar/broadleaf	1	0	2
Broadleaf	0	2	0
Broadleaf/Douglas-fir	0	1	1
Broadleaf/amabilis fir	1	1	1

[a] Broadleaf includes red alder (*Alnus rubra*) or bigleaf maple (*Acer macrophyllum*).
[b] *Picea sitchensis*.

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